
BIODIVERSITY AND CYTOGENETICS OF THE TARWEEDS (ASTERACEAE: HELIANTHEAE–MADIINAE)¹

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ABSTRACT

Because the tarweeds (Madiinae) attracted the attention of early pioneers in the areas of genecology and biosystematics, this assemblage of plants has been studied more intensively than most comparably sized groups. The tarweeds comprise 127 species in 17 genera, with centers of diversity in California and Hawaii. The biological diversity of the tarweeds is extreme. The Hawaiian members alone include herbaceous mat-forming plants, cushion plants, monocarpic and polycarpic shrubs, trees, and lianas. Collectively, the group includes self-compatible and self-incompatible annuals and perennials. An extremely conspicuous component of the diversification of tarweeds has been chromosome evolution such that gametic numbers of $n = 4-14, 16, 17, 24,$ and 34 are represented by one or more taxa. An analysis of this variation suggests that the ancestral chromosome number in the Madiinae is $n = 7$. The numerous infrageneric and nine intergeneric hybrid combinations known in the Madiinae are summarized. Among the latter hybrids, one indicates a close relationship between *Raillardiopsis muirii* and *Madia bolanderi*, and another establishes a genetic link between the mainland and Hawaiian representatives of the group.

The tarweed subtribe (Madiinae) of the sunflower tribe Heliantheae has been subjected to intensive biosystematic investigations for over 75 years. The tarweeds first captured the attention of the innovative experimental systematist H. M. Hall in 1912. In 1915, Hall enlisted the efforts of E. B. Babcock in a comprehensive treatment of the hay-field tarweeds (Babcock & Hall, 1924). The early tarweed studies were carried out at the University of California, but Hall joined the Carnegie Institution of Washington in 1919, and the center of tarweed research eventually shifted to Stanford. Before his death, Hall was able to welcome Jens Clausen to the growing staff of the Division of Plant Biology of the Carnegie Institution at Stanford. Clausen, working with D. D. Keck and W. M. Hiesey, initiated a series of extensive investigations into the biology of the dozen or so genera of tarweeds they recognized. These investigations continued to produce tremendously valuable and voluminous data over the next two decades. Most of this information is summarized in Clausen's *Stages in the Evolution of Plant Species* (1951).

Although little biosystematic research on the tarweeds was conducted in the 20 years following the peak of activity by Clausen, Keck, and Hiesey, another researcher, Sherwin Carlquist, began to study tarweeds from a different perspective. Carlquist's studies emphasized anatomical obser-

vations that led him to interpret the tarweeds as a rather closely knit group that includes a number of genera not previously considered to belong to the Madiinae, i.e., *Raillardella* (including *Raillardiopsis*) from western North America and *Argyroxiphium*, *Dubautia*, and *Wilkesia* from Hawaii (Carlquist, 1959). Carlquist's position on the last-mentioned three genera is of special significance because Keck (1936a, b) had specifically denied any close relationship between the Hawaiian genera and the Pacific coast tarweeds. Carlquist further stimulated interest in the Hawaiian genera in his *Hawaii, A Natural History* (1970).

Beginning about 20 years ago, biosystematic interest in the Madiinae was again on the rise. Research during this period produced a considerable amount of new biosystematic information, particularly in the Hawaiian genera and in the mainland genera *Calycadenia*, *Hemizonia*, *Holocarpha*, *Lagophylla*, and *Layia* (e.g., Carr, 1975a, b, 1977, 1985a; Carr & Carr, 1983; Carr & Kyhos, 1981, 1986; Gottlieb & Ford, 1987; Palmer, 1982; Tanowitz, 1977, 1978, 1982, 1985; Tanowitz & Adams, 1987; Thompson, 1983). The purpose of this paper is to survey briefly the diversity of the Madiinae, to summarize and integrate existing biosystematic information (some from unpublished dissertations), and to provide a preview of the results of ongoing biosystematic efforts within

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TABLE 1. Characteristics of the genera of Madiinae.

Genera	Numbers of species	Haploid chromosome numbers ¹	Descriptions ²
PERENNIAL			
<i>Adenothamnus</i>	1	14	Small evergreen subshrubs, SI
<i>Argyroxiphium</i>	5	14	Polycarpic and monocarpic rosette shrubs, SI, SC
<i>Dubautia</i>	21	13(9), 14(12)	Subherbaceous mats, cushions, shrubs, trees, lianas, SI, SC?
<i>Holozonia</i>	1	14	Mesophytic herbs with fleshy rhizomes, SI
<i>Raillardella</i>	3	17(1), 17, 18?(1), 34(1)	Mat-forming or spreading scapose rhizomatous herbs of high elevations, SI
<i>Raillardiopsis</i>	2	7(1), 8(1)	Tufted to mat-forming rhizomatous herbs of high elevations, SI, SC?
<i>Wilkesia</i>	2	14	Polycarpic and monocarpic rosette shrubs, SI
TRANSITIONAL ³			
<i>Hemizonia</i>	6P, 27A	9(4), 10(2), 11(4), 12(11), 13(3), 14(7)	Mostly late-flowering xerophytic herbs, the perennials subshrubby or rhizomatous, SI
<i>Madia</i>	2P, 18A	6(1), 7(1), 8(6), 9(3), 14(1), 16(5), 16, 24(1), 24(1)	Mesophytic to xerophytic herbs, the perennials with woody rhizomes, SC, SI
ANNUAL			
<i>Achyrachaena</i>	1	8	Small vernal mesophytic herbs, SC
<i>Blepharipappus</i>	1	8	Small xerophytic herbs, SI
<i>Blepharizonia</i>	1	14	Stout, xerophytic, late-flowering herbs, SI?
<i>Calycadenia</i>	11	4(1), 5, 6(1), 6(4), 7(5)	Mostly late-flowering xerophytic herbs, SI, SC
<i>Holocarpa</i>	4	4(1), 4, 5?(1), 4?, 6(1), 6(1)	Mostly late-flowering xerophytic herbs, SI
<i>Lagophylla</i>	4	7	Mesophytic to xerophytic herbs, SI, SC
<i>Layia</i>	16	7(6), 8(8), 16(1)	Vernal herbs, SI, SC
<i>Osmadenia</i>	1	9	Highly branched herbs, SI

¹ The information on chromosome numbers is a compilation of those given by Carlquist, 1959; Carr, 1975a, b, 1977, 1978, 1985; Clausen, 1951; Clausen et al., 1932, 1933, 1934, 1935, 1936, 1937, 1940, 1941, 1945; Johansen, 1933; Keck, 1949, 1958, 1959; Kyhos (in Carlquist, 1959); Strother (in Ferlatte, 1978), 1983; Tanowitz, 1982; Venkatesh, 1958; and previously unreported counts of $n = 12$ for *Hemizonia frutescens* A. Gray based on root tip squashes of living material collected from Guadalupe Island, Mexico by Bruce Baldwin (*Baldwin & Beauchamp* 688 in DAV), and $n = 9$ for *Madia doris-nilesiae* T. W. Nelson & J. P. Nelson from bud material collected from Trinity County, California, by Barbara Williams (*Williams* 518). In genera where there is variation in chromosome numbers, the number of species with a particular chromosome constitution is given in parentheses.

² SC = self-compatible; SC? = self-compatible or partially so; SI = self-incompatible; SI? = self-incompatible or partially so.

³ The two genera in this category contain perennial (P) and annual (A) species as indicated in the second column.

this fascinating group of plants. Details of other current research on the tarweeds are summarized elsewhere (e.g., flavonoid chemistry—Crins & Bohm, this volume; enzyme electrophoresis—Witter, this volume; physiological ecology—Robichaux et al., this volume; chloroplast DNA evolution—Baldwin et al., this volume).

TARWEED CHARACTERISTICS

The name tarweed refers to the often copious sticky glandular secretions produced on the surfaces of these plants, especially in the regions of the capitulescences. As viewed herein, the tarweed group (Madiinae) comprise 127 species in 17 gen-

era, six of which are monotypic (Table 1). Seven genera are wholly perennial, eight are wholly annual, and two include annual and perennial species. While all of the 28 Hawaiian species are perennial, only 15 perennials are found among the 99 species from the Pacific coast of the Americas.

The annual species of mainland tarweeds range from about 2 cm in *Madia minima* (A. Gray) Keck to 2.5 m tall in *M. elegans* D. Don ex Lindley subsp. *densifolia* (E. Greene) Keck (Keck, 1959). The perennial mainland taxa comprise small evergreen or deciduous subshrubs and herbaceous rhizomatous taxa, some of which form extensive mats (e.g., *Raillardella* species). In contrast, the

Hawaiian taxa are exceedingly diverse and include a mat-forming subshrub, *Dubautia scabra* (DC.) Keck; a cushion plant, *D. waialealae* Rock; monocarpic and polycarpic rosette shrubs, e.g., *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat and *Wilkesia hobyi* H. St. John; woody shrubs, e.g., *D. plantaginea* Gaudich.; trees, e.g., *D. reticulata* (Sherff) Keck; and a liana, *D. latifolia* (A. Gray) Keck (Carr, 1985a).

Although there are some exceptions, the leaves of mainland tarweeds are typically narrow and somewhat linear, often grasslike in general appearance. The Hawaiian assemblage includes this type but in many species the leaves are much broader (Carr et al., 1989). The leaf veins frequently exhibit a somewhat parallel orientation that becomes extreme and exceedingly grasslike in *Wilkesia* species. However, the leaves of *Dubautia latifolia* exhibit a highly isodiametrically reticulate venation that contrasts sharply with the situation in *Wilkesia* (Carr, 1985a). In general, the leaves of vernal flowering mainland taxa such as *Layia* or plants of comparatively wet habitats in Hawaii are larger and more mesomorphic compared to those of late-flowering mainland taxa such as *Holocarpha* or Hawaiian taxa occurring in dry habitats (Carr et al., 1989). In surface area the leaves range from about 0.1 to 75 cm².

The flowering heads of tarweeds range from small and inconspicuous (4 mm high and less than 2 mm broad) in *Calycadenia hooveri* G. Carr and *Dubautia pauciflora* H. St. John & G. Carr, with two or three florets per capitulum, to large and showy (35 mm tall and 60 mm broad) in *Adenothamnus validus* (Brandege) Keck and *Argyroxiphium sandwicense* subsp. *macrocephalum*, the latter with up to 650 florets per capitulum. Almost all of the mainland taxa have radiate flowering heads, whereas in Hawaii, rays are found in the heads of only five of the 28 species. Flower colors are white, red, orange, yellow, or combinations thereof.

The mainland tarweeds occur almost exclusively in the western U.S., with their distributional center in the central valley of California. A few species extend into Mexico, and a few others are restricted to the Mexican mainland or offshore islands. Two highly disjunct species are found in South America (Chile and Argentina). The mainland perennial species are mostly quite rare and restricted in distribution, suggesting that they may be relicts of an ancestral plexus.

A second center of diversity of tarweeds is the Hawaiian archipelago, where representatives of the group occur on all of the major islands including

Hawaii, Maui, Lanai, Molokai, Oahu, and Kauai. All of the tarweed species in the Hawaiian Islands are included in the Hawaiian endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia*.

The mainland tarweeds are at home in lowland, sometimes quite xeric habitats; however, some species are found above timberline (e.g., *Raillardella argentea*); and *Madia bolanderi* (A. Gray) A. Gray typically occurs in very wet mid-elevation habitats. The Hawaiian representatives occur in tremendously diverse habitats, including recent lava flows, cinder cones, dry scrub, dry forests, mesic forests, rainforests, and bogs. Annual precipitation in these habitats ranges from about 35 cm to over 12 m. Hawaiian tarweed sites are found from near sea level to about 3,750 m elevation.

The annual mainland species generally germinate during the period of winter rains, persisting as rosettes until bolting and flowering occurs. In many species this takes place in late summer or fall, and it is not uncommon to find tarweeds flowering during October and November, or even December, before the winter rains of the following season. At the other extreme, *Achyrrachaena mollis* Schauer and most species of *Layia*, among others, are vernal in their growth and flowering responses. The perennials are less predictable, although even in Hawaii they are mostly seasonal in their flowering, with summer flowering most common. A few species, such as *Dubautia knudsenii* Hillebrand, flower more or less continuously throughout the year.

As a result of the long period of intensive biosystematic research on tarweeds, the chromosome numbers are known for 122 (over 96%) of the 127 species. The only species for which no chromosome information is available are *Argyroxiphium virescens* Hillebrand (presumed extinct), *Hemizonia martirensis* Keck, *H. streetsii* A. Gray, *Layia ziegleri* Munz, and *Madia stebbinsii* T. W. Nelson & J. P. Nelson. *Calycadenia*, *Madia*, and *Hemizonia* are the most diverse in chromosome number, and together with *Raillardella*, include all of the different numbers found in the entire subtribe (Table 1). Eight of the genera have only a single confirmed chromosome number. Among the perennials, chromosome numbers are $n = 6, 7, 8, 12, 13, 14, 17,$ and 34 , whereas the annuals are somewhat more diverse in chromosome numbers with $n = 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16,$ and 24 (Tables 1, 2). Some species have more than one chromosome number, such as *Calycadenia pauciflora* A. Gray ($n = 5, 6$; Carr, 1975b) and *Madia gracilis* (Smith) Keck ($n = 16, 24$; Clausen et al., 1945). Mixed chromosome

TABLE 2. Distribution of Madiinae taxa in relation to gametic chromosome numbers.¹

<i>n</i> = 4	5	6	7	8	9	10	11	12	13	14	15	16	17	24	34
			P	P										ALL SPECIES	
			P	A											
			A	A											
			A	A											
			A	A											
			A	A						18PH					
			A	A				P		P					
			A	A				P		P					
			A	A				P		P					
			A	A	A			P		A					
		P	A	A	A			P		A					
		A	A	A	A			P		A					
		A	A	A	A			P		A					
		A	A	A	A			P		A					
A		A	A	A	A		A	A	9ph	A					
A		A	A	A	A	A	A	A	A	A				P	A
A	A	A	A	A	A	A	A	A	A	A			P	A	P
			P	P						3PH				ALL GENERA ²	
			AP	AP						P					
		AP	A	A	AP					AP					
A		A	A	A	AP				ph	AP		A			
A	A	A	A	A	A	AP	AP	AP	AP	A		AP	P	A	P
			AP	P	P			AP	ph	3PH				PERENNIAL GENERA ³	
			P	P					AP	P					
			P	P						P					
<i>n</i> = 4	5	6	7	8	9	10	11	12	13	14	15	16	17	24	34

¹ A = annual, P = perennial, AP = both annual and perennial, PH = perennial Hawaiian taxon, ph = derived perennial Hawaiian taxon; **boldfaced** entries represent *Hemizonia*.

² Several genera are represented in more than one category.

³ Includes perennial component of genera with both annual and perennial species. Some genera are represented in more than one category.

numbers showing apparent polyploid relationships within genera have turned up in *Layia*, *Madia*, and *Raillardella*.

One report of *n* = 18 for *Raillardella argentea* A. Gray from San Geronio Pass in southern California (Kyhos, in Carlquist, 1959) differs from those determined for this species from other locations in the Sierra Nevada (*n* = 17; Strother, 1983; *n* = 17; Kyhos, unpublished) and represents a number not otherwise known in this genus. The erroneous report of *n* = 16 by Powell & Powell (1978) for *Raillardopsis muirii* (A. Gray) Rydb. (as *Raillardella muirii*) was apparently based on a miscommunication of the much earlier determination of *2n* = 16 by Kyhos (in Carlquist, 1959). Similarly, the report of *n* = 18 for *Raillardella argentea* by the same authors was apparently based on the earlier determination for this taxon by Kyhos

(in Carlquist, 1959). Powell & Powell (1978) provided the locality and voucher information for the material on which Kyhos's determinations were made. Idiograms depicting *n* = 5 in *Holocarpa virgata* (A. Gray) Keck and *n* = 4 in *H. obconica* (Clausen & Keck) Keck by Clausen (1951) represent numbers not otherwise known for these species and need further documentation.

Very few plant groups of comparable size are better known cytologically. An examination of the pattern of distribution of the 122 species in Madiinae with known chromosome numbers reveals very prominent modes at *n* = 7 and *n* = 8, lesser modes at *n* = 12 and *n* = 14 (if one deemphasizes the monophyletic Hawaiian taxa), and minor peaks at *n* = 6, 9, and 16 (Table 2, top). This extensive and somewhat complex distribution pattern is open to various interpretations.

The pattern is simpler and less ambiguous if the chromosome number variation is considered at the generic level, where the several modes observed at the species level condense to a relatively uncomplicated pattern (Table 2, middle). This simplification is due in large measure to elimination of the influence of single-chromosome-number clusters of closely related species. This perspective at the generic level reveals more clearly how chromosome numbers correlate with major units of morphological diversity and therefore probably provides a more accurate evolutionary and systematic understanding of the Madiinae.

At the generic level the prominent modes at $n = 7$ and $n = 8$ are still present, and the only other well-developed mode is at $n = 14$ (Table 2, middle). This $n = 14$ mode consists of five quite distinct mainland genera in addition to three mutually closely related Hawaiian genera. In contrast, the $n = 16$ mode, consisting of a small cluster of closely related annual autogamous species of *Madia* and *Layia*, represents much less diversity. Of the two genera at $n = 13$, one is Hawaiian (*Dubautia*) and consists of species known to be derived from members of Hawaiian Madiinae with $n = 14$ (Carr & Kyhos, 1981, 1986) and the other is *Hemizonia*, represented by three fairly closely related species. With these three exceptions, each gametic chromosome number from $n = 10$ upward is represented by only a single genus.

Thus, the relatively simple picture that emerges at the generic level supports the view that the majority of the polyploid taxa within Madiinae are based on $n = 7$ and that although $n = 8$ is well represented at the diploid level, its polyploid derivatives are few. This suggests that $n = 7$ is of greater antiquity in the subtribe and perhaps depicts the ancestral chromosome number for Madiinae.

When *Hemizonia* is omitted from the total array of chromosome numbers (Table 2) a very large gap appears in the overall distribution of chromosome numbers, such that no taxa are represented at $n = 10, 11, 12,$ and 13 (except the Hawaiian derivatives). All of the remaining species or genera fall into two quite discrete groups, one consisting of apparent diploids with gametic chromosome numbers ranging continuously from $n = 4$ to $n = 9$ and a second group composed of what appear to be polyploid taxa with gametic chromosome numbers of $n = (13), 14, 16, 17, 24,$ and 34 (Table 2). With its 33 species, *Hemizonia* is the largest genus in Madiinae, making up almost 26% of the subtribe. On this basis alone, one might predict that its removal is likely to have a pro-

nounced effect on the overall pattern of chromosome number distribution in Madiinae. Nevertheless, it seems quite significant that the removal of no other single genus or even any combination of genera cleaves the rest of the tribe into separate diploid and polyploid groups. *Hemizonia* includes a continuous series of gametic chromosome numbers ranging from $n = 9$ to $n = 14$, and it modally centers at $n = 12$. This may indicate that the genus is primitively polyploid and that gametic chromosome numbers above and below $n = 12$ represent aneuploid derivatives from this polyploid mode.

The distribution pattern of gametic chromosome numbers of the perennial genera within Madiinae is quite similar to that of the entire subtribe (Table 2, bottom). When the perennial taxa are examined at either the specific or generic level, a small mode appears at $n = 7$ and a more prominent mode is present at $n = 14$. If one accepts the reasonable assumption that the ancestral taxa to the tribe are more likely to have been perennials, it seems particularly significant that the chromosome number distribution of the extant perennials conforms to the previous pattern observed for the entire subtribe in that the polyploids are concentrated at $n = 14$ and thus appear to be based principally on $n = 7$, not on $n = 8$. This interpretation is supported further by the total absence of perennial taxa with $n = 16$. On the other hand, the possibility cannot be dismissed that the prominence of $n = 14$ taxa within the subtribe may at least in some cases be the result of the combination of diploid species with $n = 6$ and $n = 8$ to produce polyploids at $n = 14$. This possibility is strengthened by preliminary evidence obtained from hybridization experiments involving the Hawaiian and mainland Madiinae (Baldwin, 1989; Baldwin et al., unpublished).

INFRAGENERIC CYTOGENETIC RELATIONSHIPS

With the exceptions of *Wilkesia* and monospecific genera, one or more interspecific hybrids have been produced in all of the tarweed genera. The cytogenetic information on these hybrids is summarized below according to the sequence of genera in Table 1.

GENERA WITH PERENNIAL SPECIES ONLY

Argyroxiphium. *Argyroxiphium* comprises five perennial species, all with $n = 14$ (Table 1). Only the interspecific combination *A. grayanum* (Hillebrand) Degener \times *A. sandwicense* subsp. *sandwicense* has been produced (Carr & Kyhos, 1986). The two F_1 individuals available for analysis

averaged 63% pollen stainability and consistently produced 12 pairs and one chain or ring of four chromosomes at meiosis, indicating heterozygosity for a single reciprocal chromosome translocation. In spite of its heterozygosity, this hybrid functioned well as a male and as a female parent in the production of an intergeneric recombinant involving *Dubautia linearis* (Gaudich.) Keck. Self-incompatibility has been demonstrated in *A. sandwicense* (Carr et al., 1986).

Dubautia. The wholly perennial genus *Dubautia* includes nine species with $n = 13$ and 12 species with $n = 14$ (Table 1). A total of 41 different interspecific hybrid combinations, 11 of them occurring in nature, have been available for study (cf. Carr & Kyhos, 1986). Chromosome structural stability among the 13-paired species of the genus is indicated by the consistent meiotic display of 13 pairs of chromosomes and high pollen stainability (96% or greater) of all interspecific hybrid combinations involving these species. The close relationship between the genome of *D. scabra* ($n = 14$) and the 13-paired genome is demonstrated by consistent production of 12 pairs and one chain of three chromosomes during meiosis and the high pollen stainability averaging 81% in 29 individuals of seven different interspecific combinations involving *D. scabra* and 13-paired species. Cytogenetic, biogeographic, and morphological evidence, as well as information from isozyme studies (Witter, this volume; Witter & Carr, 1988) support the conclusion that the 13-paired species represent a monophyletic group comparatively recently derived via aneuploid reduction of chromosomes from the $n = 14$ genome possessed by *Dubautia scabra*.

Unlike the 13-paired genome, the 14-paired genome is not structurally uniform. Biosystematic studies have so far revealed four $n = 14$ chromosome structural cytotypes comprising one or more highly morphologically differentiated species that differ from one another by a minimum of one or two reciprocal translocations, as indicated by the meiotic configurations in different interspecific hybrid combinations. Pollen stainability in these hybrids ranges from 27% to 42% and appears to be determined largely by the complexity and behavior of the multiple chromosome associations. A single univalent chromosome resulting from chiasma failure in one of the chromosome multiples may be seen in a low frequency of meiocytes in some of these hybrids. The cytogenetic evidence indicates that a limited number of chromosomes have been repeatedly involved in separate translocation

events to produce the observed spectrum of cytotypes.

It has been possible to create a number of hybrid products beyond the F_1 generation. In one instance, two interspecific hybrids involving species with the same chromosome structural arrangement were crossed to produce a hybrid product combining the four species *Dubautia knudsenii*, *D. laxa* Hook. & Arn., *D. microcephala* Skotts., and *D. plantaginea*. In another example, three chromosomally differentiated species, *D. knudsenii* ($n = 14$), *D. latifolia* ($n = 14$), and *D. sherffiana* Fosb. ($n = 13$) were combined in two successive hybridizations. Clearly, results to date suggest that it is possible to hybridize and potentially to recombine virtually any combination of species in the genus regardless of their exceedingly diverse morphological and chromosomal attributes. Self-incompatibility and self-compatibility occur in the genus (Carr et al., 1986).

Raillardella. Three perennial species comprise the genus *Raillardella* (Table 1). Two interspecific hybrid combinations, *R. pringlei* E. Greene ($n = 17$) \times *R. scaposa* A. Gray ($n = 34$) and *R. pringlei* \times *R. argentea* (A. Gray) A. Gray ($n = 17$), have been produced (Baldwin, 1989). At meiosis the first hybrid exhibited a mixture of univalents, bivalents, trivalents, and possibly larger chromosome multiples, whereas the second hybrid exhibited only normal meiotic bivalents. Experience with cultivated plants suggests that all three species in the genus are self-incompatible.

Raillardopsis. *Raillardopsis* consists of two perennial species. One hybrid between *R. muirii* ($n = 8$) and *R. scabrida* (Eastw.) Rydb. ($n = 7$) exhibited mostly univalents and chains of chromosomes at meiosis. The spectrum of multiple associations observed in the hybrid indicates that the parental genomes are differentiated by at least three chromosome translocations (Baldwin, 1989). Stainable pollen grains in this hybrid (9%) were mostly four-colporate, suggesting a derivation from unreduced meiocytes. Experimental manipulations indicate that *R. muirii* is self-incompatible (Baldwin & Kyhos, in press) and suggest that *R. scabrida* may have limited self-compatibility.

GENERA WITH PERENNIAL AND ANNUAL SPECIES

Hemizonia. The largest genus of Madiinae is *Hemizonia* with 27 annual and six perennial species (Table 1). The perennial species are all highly restricted in distribution and most are quite rare. They occur principally on the offshore islands of

southern California and Baja California Norte, although *H. minthornii* Jepson and *H. perennis* (E. Greene) Keck are confined to the mainland in coastal and near-coastal habitats. The otherwise insular *H. greeneana* Rose has a narrowly restricted extension on the mainland of Baja California at Punta Banda. Nearly all of the annual species of *Hemizonia* are confined to the mainland of California, with a few extending into the adjacent western states and Mexico. In contrast to the characteristically rare and restricted perennial species, which appear to be relictual, many of the annual species of *Hemizonia* are quite common, relatively widespread, and thus apparently vigorous, recently evolved entities.

Most of what is known biosystematically about *Hemizonia* has been derived from the extensive research conducted by Clausen, Keck, and Hiesey in the first half of this century (Clausen, 1951). Subsequently, Tanowitz (1977, 1978, 1982, 1985) generated additional biosystematic information for the genus. The species of *Hemizonia* appear to form four rather natural species groups or sections, which have been given various names by different taxonomists. Section *Hemizonia* (formerly sect. *Euhemizonia*) consists of seven species, each with 14 pairs of chromosomes, which sets them apart from all other species in the genus. The Carnegie research team found that these seven species could all be intercrossed easily and that their hybrids represent the most fertile interspecific combinations in *Hemizonia*. Section *Centromadia*, commonly known as the spikeweeds, is an obviously natural group of four or so species that can all be intercrossed readily to produce hybrids of moderate fertility in most cases. The Carnegie research team studied four annual species of this section. These few species were found to possess a surprisingly extensive series of chromosome numbers ($n = 9, 11, 12,$ and 13). One extremely rare spikeweed, *H. perennis*, which apparently was unknown to Clausen's research group, is a rhizomatous perennial and has subsequently been investigated experimentally. It has 13 pairs of chromosomes and the ability to cross with the annual spikeweeds to produce vigorous hybrids generally with rather low fertility (Kyhos, unpublished). The third species group within *Hemizonia* consists of all the remaining annual species. These have gametic chromosome numbers that range continuously from $n = 9$ to $n = 13$. The fourth species group consists of five of the six perennial species (excluding *H. perennis*) discussed above. This group is characterized by the chromosome number $n = 12$.

The view that emerges from these experimental

studies is that most interspecific crosses within this genus produce hybrids with low to extremely low fertility (see fig. 62, Clausen, 1951). Interspecific hybrids with normal to near normal fertility are exceptional. Often the reduced fertility appears to result from chromosome differences between the species, but in some instances genetic factors are likely to be responsible. Almost half of the more than 55 interspecific combinations produced by the Carnegie research effort were highly sterile hybrids. Most of the remaining hybrid combinations had substantially depressed fertility. Intersectional hybrids typically were extremely sterile, with but a single exception involving *H. pungens* (Hook. & Arn.) Torrey & A. Gray and *H. ramosissima* Benth. (*H. fasciculata*). Some 20 interspecific hybrid combinations attempted by the Carnegie research team failed. Thus experimental evidence reveals strong reproductive barriers between most *Hemizonia* species.

A high degree of chromosome repatterning within *Hemizonia* is clearly indicated by an extensive series of chromosome numbers, which range continuously from $n = 9$ to $n = 14$. The annual species show the greatest diversity with their members spanning this entire series. The perennials are much more limited, with five of their six species having $n = 12$, and the remaining species, *H. perennis*, with $n = 13$. Unquestionably, chromosome evolution has played a major role in the evolution of the genus.

Madia. *Madia* includes some 20 species (18 annuals). The modal chromosome number is $n = 8$, but numbers of $n = 9, 14, 16,$ and 24 are also found among the annual species (Table 1). The two rhizomatous perennial species, *M. madioides* (Nutt.) E. Greene ($n = 7$) and *M. bolanderi* ($n = 6$), are chromosomally unique within the genus. As with *Layia*, nearly all in-depth biosystematic knowledge of *Madia* stems from Clausen, Keck, and Hiesey (Clausen, 1951). They produced 22 interspecific hybrid combinations among the 14 species in their crossing program. Their research revealed that the diploid species generally are strongly isolated from one another reproductively; this isolation often seems to be associated with chromosome repatterning, as is evident from the diversity of chromosome numbers in *Madia*. Some polyploid species retain substantial ability to exchange genes.

GENERA WITH ANNUAL SPECIES ONLY

Calycadenia. This genus comprises 11 annual species with chromosome numbers ranging from n

= 4 to $n = 7$ (Table 1). Seventeen interspecific hybrid combinations have been examined (Carr, 1975a, 1977). Hybrids among the seven-paired species *C. mollis* A. Gray, *C. truncata* DC., and *C. villosa* DC. are very sterile, exhibiting less than 1% stainable pollen grains, and are characterized by very low meiotic pairing of chromosomes. The hybrid between the two seven-paired species *C. villosa* and *C. hooveri* also has less than 1% stainable pollen but often produces five pairs and one ring or chain of four chromosomes, indicating heterozygosity for a reciprocal chromosome translocation. This hybrid was also heterozygous for at least one paracentric inversion, as indicated by bridge and fragment configurations in 26% of the meiocytes. Hybrids among *C. ciliosa* E. Greene ($n = 6$), *C. hispida* (E. Greene) E. Greene ($n = 6$), *C. multiglandulosa* DC. ($n = 6$), *C. pauciflora* ($n = 5, 6$), *C. oppositifolia* (E. Greene) E. Greene ($n = 7$), and *C. spicata* (E. Greene) E. Greene ($n = 4$) are characterized by strict meiotic bivalent formation or, more frequently, large multiple associations of chromosomes, indicating structural heterozygosity for three or more reciprocal chromosome translocations in some cases. Pollen stainability in these hybrids ranged from less than 1% to 69%. A single hybrid between the seven-paired *C. villosa* and a six-paired representative of *C. pauciflora* had a pollen stainability of less than 1%. Based on a maximum meiotic association of nine chromosomes and the appearance of bridge and fragment configurations in 66% of the meiocytes of this hybrid, it was heterozygous for at least three reciprocal chromosome translocations and probably multiple paracentric inversions.

Two closely related species complexes, *Calycadenia hispida*-*C. multiglandulosa* and *C. ciliosa*-*C. pauciflora*, exhibit very different modes of evolution. The former complex is made up of five morphologically differentiated but chromosomally stable and highly interfertile taxa, while the latter complex comprises at least eleven mostly somewhat morphologically cryptic chromosome races differentiated from one another by reciprocal chromosome translocations and in some cases at least one pericentric inversion (Carr, 1975b, 1977; Carr & Carr, 1983). There appear to be no significant differences in reproductive biology, numbers of chromosome mutations detected in field populations, habitats, flowering times, or chiasma frequencies that might provide a basis for the very different modes of evolution observed in these two species complexes. These differences may be attributable to the importance of gene position (pattern) effects and/or gene linkage effects in pro-

ducing optimum genomic arrangements in these plants (Kyhos & Carr, unpublished).

Over 500 interpopulational hybrids in more than 300 progenies have led to the recognition of four homoploid races ($n = 6$) and one heteroploid race ($n = 5$) in *Calycadenia pauciflora* and five homoploid races in *C. ciliosa* ($n = 6$) (Carr, 1975b; Carr & Carr, 1983). Ongoing research with additional hybrids indicates further unresolved complexity in *C. ciliosa* and one additional race ($n = 6$) of *C. pauciflora* (Carr & Carr, unpublished). The evidence suggests that a six-paired race of *C. pauciflora* arose from *C. ciliosa*, underwent additional chromosome repatterning, and ultimately produced the five-paired race by aneuploid reduction.

The research with *Calycadenia ciliosa* has revealed extremely high levels of chromosome structural heterozygosity among individuals of three populations. In one population, 30% of the plants sampled were heterozygous for one or two translocations or a pericentric inversion. In another population, morphologically indistinguishable plants within 100 m of one another were differentiated by a minimum of four reciprocal chromosome translocations (Carr & Carr, 1983).

Other current research reveals the presence of at least three structurally differentiated genomes in *C. truncata*. Extensive biosystematic manipulations with all species of the genus have demonstrated strict self-incompatibility in all but *C. hooveri* and one population of *C. truncata*.

Holocarpa. Despite being a small genus of four annual species, the taxa of *Holocarpa* present a very complex situation in terms of chromosome repatterning and reproductive isolation. This extreme complexity was first revealed by Clausen, Keck, and Hiesey in the 1930s and 1940s (Clausen, 1951). The initial indication of the complexities within this genus was the discovery that *H. macradenia* (DC.) E. Greene and *H. virgata* have a chromosome number of $n = 4$, whereas *H. obconica* and *H. heermannii* (E. Greene) Keck have $n = 6$. It was further recognized that three of these species, exempting *H. macradenia*, displayed considerable intraspecific karyotypic variation, indicative of substantial chromosome evolution among and within the species. Clausen (1951) expressed the opinion that the rare *H. macradenia* had probably already become extinct, which may be the reason it was not studied more thoroughly.

However, subsequent research by Palmer (1982) revealed that *H. macradenia*, although near extinction, survived in seven small, widely scattered

populations in the San Francisco Bay and Monterey Bay regions. Five of these relict populations remain today. Palmer showed that the then-extant seven relict populations were cross-compatible, interfertile, and in possession of the same chromosome arrangement, with the exception of a single population near Santa Cruz. This exceptional population differs from the others primarily by a chromosome translocation, with a second translocation also possibly present in some members of the population. All tested individuals of *H. macradenia* are self-incompatible, as are the other three species of *Holocarpha*. Some populations of the chromosomally diverse *H. virgata* differ from the modal chromosome arrangement of *H. macradenia* by only a single translocation and thus produce interspecific hybrids with *H. macradenia* that are upward of 80% fertile.

Palmer's (1982) research also revealed a fairly close relationship between *H. macradenia* ($n = 4$) and *H. heermannii* ($n = 6$) in that their interspecific hybrid at meiosis forms a chromosome pairing configuration of a multiple of six and multiple of four. Similarly, Palmer turned up a close relationship between *H. macradenia* and *H. obconica* ($n = 6$), their interspecific hybrid producing a configuration of three pairs and a multiple of four chromosomes at meiosis.

Lagophylla. This is a small genus of four annual species, all with a chromosome number of $n = 7$. Biosystematic investigations (Thompson, 1983) showed these species to be differentiated from one another by one or two reciprocal chromosome translocations and in some instances by inversions. This relatively modest amount of chromosome re-patterning seems to be responsible for the reduced fertility observed in all interspecific hybrids. Fertility in these hybrids modally ranges from values as low as 15% to 25% in some interspecific combinations to as high as 40% to 60% in others. *Lagophylla dichotoma* Benth., *L. glandulosa* A. Gray, and *L. minor* (Keck) Keck are self-incompatible, whereas *L. ramosissima* Nutt. readily selfs in cultivation and presumably in nature. Correlated with these breeding system differences, *L. ramosissima* failed to serve as a successful pollen parent in experimental hybridizations but did function quite well as a pistillate parent when care was taken to prevent selfing. This sort of unilateral interspecific incompatibility has been repeatedly observed between self-incompatible and selfing taxa among members of Compositae.

Species of *Lagophylla* appear to have the most specialized floral features of the entire subtribe. All populations of *Lagophylla* always possess 11 flo-

rets per capitulum, five of which are ray florets, and the remaining six are disk florets arranged as a concentric ring of five florets encircling a single central disk floret. The ray florets are strictly pistillate, whereas the disk florets are only pollen fertile, never producing viable fruits. The flowers of *Lagophylla* species open in the morning and are typically closed by midday. Within the entire Madiinae this constellation of floral features occurs only in *Lagophylla*.

Layia. This entirely annual genus contains some 16 species with chromosome numbers of $n = 7, 8,$ and 16 (Table 1). Most of the existing biosystematic knowledge of this genus was accumulated by Clausen, Keck, and Hiesey (Clausen, 1951). They produced 24 different interspecific hybrid combinations among 13 of the 14 species in their crossing program. Although very little detailed information was presented, they attributed the broad spectrum of reduced fertilities of the hybrids to the presence of variable numbers of unpaired chromosomes.

Tanowitz & Adams (1986) studied naturally occurring hybrids between the polytypic, obligately outcrossing *Layia glandulosa* (Hook.) Hook. & Arn. ($n = 8$) and the relatively uniform, self-compatible *L. paniculata* Keck ($n = 16$). As expected, this triploid hybrid has a low fertility of less than 6% and appears incapable of exchanging genes with its two parental species. The modal meiotic chromosome configuration of the triploid hybrid is eight bivalents plus eight univalents, which was interpreted as evidence that the two parental species share a common genome. An alternative interpretation based on the possibility of autosyndetic pairing among the chromosomes of *L. paniculata* is also tenable.

In-depth comparative investigations by Ford and Gottlieb involving research into the genetics and associated developmental processes of the rare serpentine endemic *L. discoidea* Keck and its probable ancestor *L. glandulosa* greatly extend the original research of Clausen, Keck, and Hiesey (Gottlieb & Ford, 1987; Ford & Gottlieb, 1989).

INTERGENERIC CYTOGENETIC RELATIONSHIPS

Argyroxiphium × *Dubautia*. Four different intergeneric F_1 hybrid combinations involving genomes 1 and 2 of *Argyroxiphium* ($n = 14$) and genomes 1, 2 (both $n = 14$), and 5 ($n = 13$) of *Dubautia* have been analyzed (Carr & Kyhos, 1986). Meiosis in each of these hybrids is characterized by a very high frequency of normal chromosome pairing and one or more multiple chro-

mosome associations. The results indicate that the parental genomes are differentiated by two or three translocations, and by aneuploidy in the hybrids involving *Dubautia* genome 5. The mean pollen stainabilities of these hybrids range from 11% to 29%. The least fertile of these, *A. sandwicense* subsp. *macrocephalum* ($n = 14$) \times *D. menziesii* (A. Gray) Keck ($n = 13$), occurs in nature and produces backcrosses under field conditions. A synthetic intergeneric hybrid combining the genomes of *D. knudsenii*, *D. laxa*, and *A. sandwicense* subsp. *macrocephalum* was produced and subsequently crossed with *D. scabra* to yield a hybrid product combining the genomes of four species (Carr & Kyhos, unpublished). In another instance, a hybrid between genomes 1 and 2 of *Argyroxiphium* ($n = 14$) was successfully crossed with genome 5 ($n = 13$) of *Dubautia* (Carr & Kyhos, 1986).

Argyroxiphium \times *Wilkesia*. Two hybrid combinations have been produced (*A. sandwicense* subsp. *macrocephalum* \times *W. gymnoxiphium* A. Gray and *A. grayanum* \times *W. hobdyi*), but neither has yet furnished material for meiotic analysis.

Calycadenia \times *Osmadenia*. *Osmadenia tenella* Nutt. has been successfully crossed with *Calycadenia truncata*, *C. mollis*, and *C. villosa* (Carr, 1977). Observations of meiosis in the last-mentioned two combinations demonstrate essentially complete lack of pairing of the parental genomes. The chromosomes of *Osmadenia* ($n = 9$) are much smaller than those of the seven-paired species of *Calycadenia*, and these size differences were very apparent at meiosis in the two intergeneric hybrid combinations examined. The hybrids exhibited less than 1% pollen stainability.

Dubautia \times *Raillardiopsis*. Recently, *D. laevigata* A. Gray ($n = 14$) was successfully crossed with *R. muirii* ($n = 8$) (Baldwin, 1989; Baldwin et al., unpublished). This represents the first hybrid produced between Hawaiian and mainland tarweeds. The cross was easy to make and the hybrids are vigorous. Analysis of root tips of the hybrids indicates that $2n = 22$ and verifies their parentage.

Dubautia \times *Wilkesia*. Hybrids between *W. gymnoxiphium* or *W. hobdyi* and *Dubautia* genomes 1 and 4 have consistently yielded a high frequency of normal pairs and either two chains of three or one chain of six chromosomes (Carr & Kyhos, 1986). The mean pollen stainability is about 29%. One or occasionally two univalents may be found in cells exhibiting incomplete synapsis of the members of the chains of three chromosomes. Univalents of a similar origin were fairly commonly observed in a small sample of meiotic material from

a hybrid between *W. gymnoxiphium* and *D. herb-stobatae* G. Carr ($n = 13$). Maximum chromosome associations in this hybrid indicate that at least two translocations differentiate the parents, as is the case in the previous examples. However, an additional chain of three chromosomes represents the aneuploid relationship of the parents in this instance. Pollen stainability of this hybrid was 16% (Carr & Kyhos, unpublished).

Hemizonia \times *Holozonia*. The very brief report by Clausen et al. (1937) of this intergeneric combination based on *Hemizonia arida* Keck ($n = 12$) \times *Holozonia filipes* (Hook. & Arn.) E. Greene ($n = 14$) appears to have been overlooked by most recent tarweed workers. Aside from noting that it is a remarkable combination involving an annual and a perennial species, Clausen et al. (1937, p. 212) did little more than characterize it as "a vigorous but sterile hybrid grown in 1937."

Layia \times *Madia*. Two hybrid combinations have been made (Clausen, 1951). The first, *M. elegans* ($n = 8$) \times *L. platyglossa* (Fischer & C. Meyer) A. Gray ($n = 7$), was extremely weak and apparently did not yield cytogenetic data. The second, *M. sativa* Molina ($n = 16$) \times *L. platyglossa* ($n = 7$), although fairly vigorous, was highly sterile as a result of its being a triploid with 23 somatic chromosomes.

Madia \times *Raillardiopsis*. Only one combination, *M. bolanderi* ($n = 6$) \times *R. muirii* ($n = 8$) has been produced (Baldwin, 1989). Hybrids of this combination exhibit a mixture of chromosome pairs, multiples, and univalents during meiosis. The multiples observed indicate that the parental genomes are differentiated by at least two reciprocal chromosome translocations. Pollen stainability of two individuals averaged 7%.

Raillardella \times *Raillardiopsis*. The single hybrid combination produced, *Raillardella pringlei* ($n = 17$) \times *Raillardiopsis muirii* ($n = 8$), exhibited mostly univalents at meiosis. Only a low frequency of cells yielded one or two pairs of chromosomes. The chromosomes fall roughly into two size classes with about eight (presumably those of *Raillardiopsis muirii*) in the large size class. The pollen stainability of this hybrid is 1% (Baldwin, 1989).

DISCUSSION

Infrageneric biosystematic and cytogenetic studies indicate that variation in chromosome number and/or structure occurs in all ten of the genera

with more than one species that have been investigated. It is clear that repatterning of chromosomes has been a very significant aspect of the overall differentiation of the tarweeds, but chromosomal and morphological diversification have frequently proceeded at very different rates. In some cases, as in *Calycadenia*, chromosomal differentiation has been pervasive and has accrued even among forms that are otherwise exceedingly similar, if not indistinguishable (Carr, 1977; Carr & Carr, 1983). Certain chromosomes have been repeatedly involved in translocations in *Calycadenia* (Carr, 1975b; Carr & Carr, 1983) and *Dubautia* (Carr & Kyhos, 1986). By comparison, the chromosomes of *Lagophylla* exhibit only modest infrageneric variation in structure (Thompson, 1983). Overall, the kinds of chromosome evolution that have been documented within the Madiinae include aneuploidy, polyploidy, and structural differentiation by way of reciprocal translocations and pericentric and paracentric inversions.

Nine different intergeneric hybrid combinations have been produced. Of the six that have been examined, pollen stainability ranges from less than 1% to 29%. Meiotic chromosome associations among the intergeneric hybrids range from essentially all univalents in most meiocytes of *Calycadenia* × *Osmadenia* to exclusively pairs and multiples in most meiocytes of *Argyroxiphium* × *Dubautia*. There appears to be very little potential for intergeneric gene flow, especially under field conditions, except between the Hawaiian genera *Argyroxiphium* and *Dubautia*.

The relatively high fertility among the Hawaiian taxa could be used to argue for their treatment as congeners. However, the three Hawaiian genera recognized here are easily distinguished and conform well to generic concepts used elsewhere in the Asteraceae (Carr, 1985b). Moreover, the argument used to reduce these taxa to a single genus could logically be extended to reduce them to a single species, an extension that even the most strict adherents to the biological species concept would have to question.

Two of the intergeneric hybrids briefly reported here establish a closeness of relationship not previously perceived for the genera involved. Furthermore, the degree of chromosome association and fertility in the first of these hybrids, *Madia* × *Raillardiopsis*, suggests that a taxonomic realignment may prove necessary. The second of these hybrids, *Dubautia laevigata* × *Raillardiopsis muirii*, establishes a direct genetic link between the mainland and Hawaiian tarweeds. Attempts to produce both hybrids were encouraged by results

from a cpDNA study that indicated very close relationship among *Madia bolanderi*, *Raillardiopsis muirii*, and the Hawaiian taxa (Baldwin, 1989; Baldwin et al., this volume). These hybrids provide the opportunity to explore the derivation of what may very well be the ancestral genomes of the entire assemblage of Hawaiian Madiinae. This may be an exciting new chapter in the rich history of biosystematic and other experimental research on the tarweeds. As Jens Clausen used to say, "We have only just begun to scratch the surface."

LITERATURE CITED

- BABCOCK, E. B. & H. M. HALL. 1924. *Hemizonia congesta*: a genetic, ecologic, and taxonomic study of the hay-field tarweeds. Univ. Calif. Publ. Bot. 13: 15–100.
- BALDWIN, B. G. 1989. Chloroplast DNA Phylogenetics and Biosystematic Studies in Madiinae (Asteraceae). Ph.D. Dissertation. Univ. of California, Davis, California.
- & D. W. KYHOS. 1990. A systematic and biogeographic review of *Raillardiopsis* [*Raillardella*] *muirii* (Madiinae–Asteraceae), with special reference to a disjunct California Coast Range population. Madroño (in press).
- CARLQUIST, S. 1959. Studies on Madinae: anatomy, cytology, and evolutionary relationships. *Aliso* 4: 171–236.
- . 1970. *Hawaii, a Natural History*. Natural History Press, New York.
- CARR, G. D. 1975a. *Calycadenia hooveri* (Asteraceae), a new tarweed from California. *Brittonia* 27: 136–141.
- . 1975b. Chromosome evolution and aneuploid reduction in *Calycadenia pauciflora* (Asteraceae). *Evolution* 29: 681–699.
- . 1977. A cytological conspectus of the genus *Calycadenia* (Asteraceae): an example of contrasting modes of evolution. *Amer. J. Bot.* 64: 694–703.
- . 1978. Chromosome numbers of Hawaiian native plants and the significance of cytology in selected taxa. *Amer. J. Bot.* 65: 236–242.
- . 1985a. A monograph of the Hawaiian Madiinae (Asteraceae): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. *Allertonia* 4: 1–123.
- . 1985b. Habitual variation in the Hawaiian Madiinae (Heliantheae) and its relevance to generic concepts in the Compositae. *Taxon* 34: 22–25.
- & D. W. KYHOS. 1981. Adaptive radiation in the Hawaiian silversword alliance (Compositae–Madiinae). I. Cytogenetics of spontaneous hybrids. *Evolution* 35: 543–556.
- & ———. 1986. Adaptive radiation in the Hawaiian silversword alliance (Compositae–Madiinae). II. Cytogenetics of artificial and natural hybrids. *Evolution* 40: 959–976.
- , E. A. POWELL & D. W. KYHOS. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): an exception to Baker's Rule. *Evolution* 40: 430–434.
- , R. H. ROBICHAUX, M. S. WITTER & D. W. KYHOS. 1989. Adaptive radiation of the Hawaiian

- silversword alliance (Compositae-Madiinae): a comparison with Hawaiian picture-winged *Drosophila*. Pp. 79-97 in L. V. Giddings, K. Y. Kaneshiro & W. W. Anderson (editors), Genetics, Speciation and the Founder Principle. Cambridge Univ. Press, Cambridge.
- CARR, R. L. & G. D. CARR. 1983. Chromosome races and structural heterozygosity in *Calycadenia ciliosa* Greene (Asteraceae). Amer. J. Bot. 70: 744-755.
- CLAUSEN, J. 1951. Stages in the Evolution of Plant Species. Cornell Univ. Press, Ithaca, New York.
- , D. D. KECK & W. M. HEUSI. 1932. Experimental taxonomy. Carnegie Inst. Washington Year Book 31: 201-205.
- , ——— & ———. 1933. Experimental taxonomy. Carnegie Inst. Washington Year Book 32: 192-196.
- , ——— & ———. 1934. Experimental taxonomy. Carnegie Inst. Washington Year Book 33: 173-177.
- , ——— & ——— [W. M. Hiesey]. 1935. Experimental taxonomy. Carnegie Inst. Washington Year Book 34: 201-206.
- , ——— & ———. 1936. Experimental taxonomy. Carnegie Inst. Washington Year Book 35: 208-214.
- , ——— & ———. 1937. Experimental taxonomy. Carnegie Inst. Washington Year Book 36: 209-214.
- , ——— & ———. 1940. Experimental taxonomy. Carnegie Inst. Washington Year Book 39: 158-163.
- , ——— & ———. 1941. Experimental taxonomy. Carnegie Inst. Washington Year Book 40: 160-170.
- , ——— & ———. 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autopolyploidy, with examples from the Madiinae. Publ. Carnegie Inst. Wash. 564: 1-174.
- FERLATTE, W. J. 1978. Notes on two rare, endemic species from the Klamath Region of northern California, *Phacelia dalesiana* (Hydrophyllaceae) and *Raillardella pringlei* (Compositae). Madroño 25: 138.
- FORD, V. S. & L. D. GOTTLIEB. 1989. Morphological evolution in *Layia* (Compositae): character recombination in hybrids between *L. discoidea* and *L. glandulosa*. Syst. Bot. 14: 284-296.
- GOTTLIEB, L. D. & V. S. FORD. 1987. Genetic and developmental studies of the absence of ray florets in *Layia discoidea*. Pp. 1-17 in H. Thomas & D. Grierson (editors), Developmental Mutants in Higher Plants. Society of Experimental Biology. Cambridge Univ. Press, Cambridge.
- JOHANSEN, D. A. 1933. Cytology of the tribe Madinae, family Compositae. Bot. Gaz. (Crawfordsville) 95: 177-208.
- KECK, D. D. 1936a. The Hawaiian silverswords: systematics, affinities, and phytogeographic problems of the genus *Argyroxiphium*. Occas. Pap. Bernice Pauahi Bishop Mus. 11: 1-38.
- . 1936b. The silverswords of Hawaii. News Serv. Bull. Carnegie Inst. Wash. 4: 75-78.
- . 1949. *Hemizonella* becomes a *Madia*. Madroño 10: 22.
- . 1958. Taxonomic notes on the California flora. Aliso 4: 101-114.
- . 1959. Madiinae. Pp. 1106-1129 in P. A. Munz (editor), A California Flora. Univ. California Press, Berkeley, California.
- PALMER, R. E. 1982. Ecological and Evolutionary Patterns in *Holocarpha* (Compositae, Madiinae). Ph.D. Dissertation. Univ. of California, Davis, California.
- POWELL, A. M. & S. A. POWELL. 1978. Chromosome numbers in Asteraceae. Madroño 25: 160-169.
- STROTHER, J. L. 1983. More chromosome studies in Compositae. Amer. J. Bot. 70: 1217-1224.
- TANOWITZ, B. D. 1977. An intersectional hybrid in *Hemizonia* (Compositae: Madiinae). Madroño 24: 55-61.
- . 1978. *Hemizonia conjugens* (Compositae): distribution, chromosome number, and relationships. Madroño 25: 159.
- . 1982. Taxonomy of *Hemizonia* sect. *Madiomeris* (Asteraceae: Madiinae). Syst. Bot. 7: 314-339.
- . 1985. Systematic studies in *Hemizonia* (Asteraceae: Madiinae): hybridization of *H. fasciculata* with *H. clementina* and *H. minthornii*. Syst. Bot. 10: 110-118.
- & J. W. Adams. 1986. Natural hybridization between *Layia glandulosa* and *L. paniculata* (Asteraceae: Madiinae). Madroño 33: 244-252.
- THOMPSON, W. C. 1983. A biosystematic study of *Lagophylla* (Compositae: Heliantheae) and related genera. Ph.D. Dissertation. Univ. of California, Davis, California.
- VENKATESH, C. S. 1958. A cyto-genetic and evolutionary study of *Hemizonia*, section *Centromadia*. Amer. J. Bot. 45: 77-84.
- WITTER, M. S. & G. D. CARR. 1988. Adaptive radiation and genetic differentiation in the Hawaiian silversword alliance (Compositae: Madiinae). Evolution 42: 1278-1287.